



TITLE:

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CITATION:

Kadowaki, Kohmei ...[et al]. Merging community assembly into the regime-shift approach for informing ecological restoration. *Ecological Indicators* 2018, 85: 991-998

ISSUE DATE:

2018-02

URL:

<http://hdl.handle.net/2433/228165>

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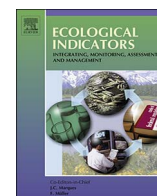
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Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Review

Merging community assembly into the regime-shift approach for informing ecological restoration



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ARTICLE INFO

Key-words:

Competition
Ecosystem functioning
Facilitation
Hysteresis
Positive feedback
Restoration
State transition

ABSTRACT

Ecosystems that exhibit alternative stable states are a prominent challenge for ecological restoration. So far, alternative stable states have been addressed from two different angles: community assembly studies, which focus on species and their interactions, and regime shift studies, which focus on changes in ecosystem states following environmental change. Here, we propose a synthetic perspective that merges the community assembly with the regime shift approach to effectively inform restoration of ecosystems exhibiting alternative stable states. We show that the community assembly and the regime shift approaches have emphasized different aspects of alternative stable states (i.e., coarse vs fine resolutions of the focal state variable, different sets of feedback mechanisms, and small vs large spatial scales), and consequently have different limitations that influence restoration strategies. Using a simple mathematical model, we illustrate that a more explicit consideration of species identity and composition (i.e., the community assembly approach) can improve our ability to understand regime shifts and restore degraded ecosystems. Finally, we highlight two case studies in which such merging can bring novel insights into alternative stable states and ecological restoration. Understanding the relevant aspects of community assembly (biotic interactions and species identity) will lead to more informed decisions that target future restoration and the prediction of regime shifts in response to global environmental change.

1. Introduction

Natural ecosystems can exhibit sudden, and sometimes unpredictable, state transitions (Scheffer et al., 2001; Suding et al., 2004). In some cases, such transition in the ecosystem state cannot be easily reversed, particularly when human activities have decreased the ecosystem's capacity to return to the original state on its own. The concept of alternative stable states, in which an ecosystem may exist in one of several possible stable states under the same range of environmental conditions, has attracted increasing interest in the literature because of the possible ecological and economic consequences that transitions between the alternative stable states may imply (Beisner et al., 2003).

Two parallel lines of research have used independent frameworks to understand different aspects of alternative stable states. *Community assembly (CA) approaches* have traditionally focused on how communities assemble through interspecific interactions and can lead to divergent species compositions as a result of different histories of

community assembly (e.g. Robinson and Dickerson, 1987; Drake, 1991; Chase, 2003; Fukami et al., 2005; Kadowaki et al., 2012; Chang and HilleRisLambers, 2016). On the other hand, *regime-shift (RS) approaches* have focused on sudden transitions and hysteresis of the states of ecosystems and communities due to environmental change (Scheffer and Carpenter, 2003; Suding et al., 2004). Thus, the CA and RS approaches have emphasized different feedback mechanisms for the occurrence of alternative stable states. The CA approach has focused on biotic interactions among species, such as competition (Drake, 1991; Kadowaki et al., 2012), and we therefore refer to the feedbacks typically investigated in the CA approach as “biotic feedbacks”. The RS approach has sought to identify possible mechanisms that accelerate the effects of environmental change, generally positive feedback mechanisms due to the modification of the abiotic environment by the biotic community component (e.g. Sasaki et al., 2008; Isbell et al., 2013). We refer to the feedbacks typically investigated in the RS approach as “abiotic feedbacks”, because it generally puts more emphasis on abiotic effects such

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as environmental modifications than the CA approach. Not all case studies strictly conform to one of these two broad categories of CA vs RS approaches, but this distinction captures most of the relevant differences between the approaches.

Generally, ecological restoration of systems potentially exhibiting alternative stable states requires a joint application of the RS and CA approaches that have focused on different component mechanisms supporting restoration success, i.e., the abiotic and biotic feedback mechanisms respectively. Studies using the RS approach are generally interested in that abiotic feedback mechanisms that can preclude restoration from a degraded state toward the original/desirable state (Suding and Hobbs, 2009). For example, in depression wetlands in south-eastern United States, species-rich herbaceous communities embedded within longleaf pine forests are maintained with prescribed fires (Martin and Kirkman, 2009). Periods of extended fire suppression, however, cause a shift in community structure from an herbaceous ground flora to one dominated by shrubs and hardwood species. After hardwood species dominance, re-introduction of fire alone does not restore previous herbaceous communities because hardwood species impede the spread of fire, which further facilitates hardwood dominance. Here, the restoration of herbaceous communities based on the RS approach involves reinstating prescribed fire (i.e., abiotic management) as well as mechanical and chemical hardwood species removal (i.e., biotic management). Thus, ecological restoration based on the RS approach generally seeks to re-establish the abiotic feedback that was present before the shift and thereby restore the original/desirable state, often by managing both abiotic and biotic factors.

Alternatively, many restoration efforts involving the introduction or removal of a species aim to re-establish the biotic feedback mechanism that steers community assembly (Young et al., 2005; Baer et al., 2015). For example, Baer et al. (2015) shows that, in tallgrass prairie, a former agricultural land may be restored to a high plant species diversity effectively by removing clonal plant species. Clonal plant species could decrease the positive influence of environmental heterogeneity on plant species coexistence and inhibit the establishment of new species that can exploit niches that may become available during community assembly. Thus, consideration of competition (i.e., biotic feedbacks) with clonal plant species that can limit seedling establishment is required to restore species-rich tallgrass prairie ecosystems (Baer et al., 2015). Thus, ecological restoration based on the CA approach aims to leverage the biotic feedbacks that maintain the original species composition of ecological community through removal or reintroduction of species.

Our distinction between the CA and the RS approaches builds on previous reviews (Beisner et al., 2003; Petraitis, 2013; Chang and HilleRisLambers, 2016), in which the CA perspective has dealt with the state transitions through community assembly under fixed environments, whereas the RS perspective has shown the effect of environmental change on state transitions. Notably, these two approaches have often been a source of confusion in uses and meanings of alternative stable states (Walker et al., 2012), sometimes dealt with as if they reflected a dichotomy in ecological thinking (Didham and Norton, 2007). Although several studies have distinguished the CA and RS approaches (Beisner et al., 2003; Petraitis, 2013; Chang and HilleRisLambers, 2016), these independent approaches have rarely been synthesized into a theoretical and practical framework for ecosystem management and restoration (but see Young et al., 2001, 2005 for exceptions).

In this article, we show that the CA and RS approaches have emphasized different aspects of alternative stable states, and consequently have different limitations that influence restoration strategies. Because ecological restoration should accompany value judgement (such as desirable versus undesirable state in terms of anthropogenic use) (Hobbs, 2007; Hobbs and Cramer, 2008) and involve ongoing environmental changes (Scheffer and Carpenter, 2003; Suding et al., 2004), both of which are key properties of the RS approach, we use the RS approach as a foundation approach. In what follows, we first present the key differences between the CA and RS approaches. We then

highlight the potential for integration of relevant aspects of the CA approach into the RS approach to develop a more complete framework for ecological restoration. We illustrate this point using a simple mathematical model and case studies from the literature.

2. Key differences between the CA and RS approaches

We summarize the four key differences between the CA and RS approaches, all of which are relevant for developing integrated perspectives for ecological restoration: (i) the resolution of the state variables studied, (ii) the types of perturbation considered, (iii) the relevant interaction types, and (iv) the spatial scales of the studies. Note that these four aspects are strongly related, and collectively characterize the two approaches to informing restoration.

2.1. The type and resolution of the state variables studied

State variables can be defined in a number of ways (e.g., population abundance, spatial coverages, organic and inorganic quantities) (Beisner et al., 2003; Petraitis, 2013), and importantly, the CA and RS approaches have used different resolutions of the state variables to represent alternative stable states (Fig. 1 top row). While CA studies often use different species compositions to represent alternative stable states (Chase, 2003; Fukami et al., 2005; Fukami, 2015), RS studies often summarize the ecosystem state using a single aggregated variable, namely functional groups or aggregated community properties such as total density or cover (Tomimatsu et al., 2013; Kéfi et al., 2016). For instance, an RS approach investigating desertification may define two alternative stable states between positive vegetation cover and zero vegetation cover (e.g., Kéfi et al., 2007); a CA approach investigating desertification may focus on transitions between different types of plant communities, so they may be different sets of alternative stable states along the transition to desertification, e.g. tree-and-grass vs grass only, and grass only vs desert; and there may even be alternative stable states between different abundances of grass. Thus far, the RS approach conventionally evaluates state variables at a coarser resolution than the CA approach.

2.2. Types of perturbations studied

Studies of the CA vs RS approaches have focused on different types of perturbations when making temporal observations of ecological dynamics (Fig. 1, middle row). RS studies typically evaluate the outcomes of abiotic environmental change that gradually decreases the system's ability to return to the original state (press perturbation) and abiotic pulse perturbation, such as a hurricane (Graham et al., 2015) and nutrient loading (Ling et al., 2009; Isbell et al., 2013; Sasaki et al., 2015). For instance, rangeland desertification may result from a mixture of intensified stock grazing (press perturbation) and drought (pulse perturbation) (van de Koppel et al., 1997). Conversely, the CA approach follows successional dynamics after a pulse perturbation (not including a press perturbation) up to the equilibrium of populations and communities (Young et al., 2001; Chang and HilleRisLambers, 2016) and then asks whether species' immigration history can cause differences in the final equilibrium states of species composition under certain environments (Fig. 1; priority effects or historical contingency in community assembly; Chase, 2003; Fukami, 2015). For example, Fukami et al. (2005) experimentally manipulated initial species composition (but not environmental conditions) and then tracked community structure in abandoned grasslands. As a whole, the RS approach tends to consider pulse and press perturbations acting in concert, whereas the CA approach typically often deals with species dynamic history after pulse perturbations (Beisner et al., 2003; Petraitis, 2013; Fig. 1). We illustrate that the community assembly history can determine the success or failure of ecosystem recovery in the next section (see upcoming 3. Illustration using a toy model).

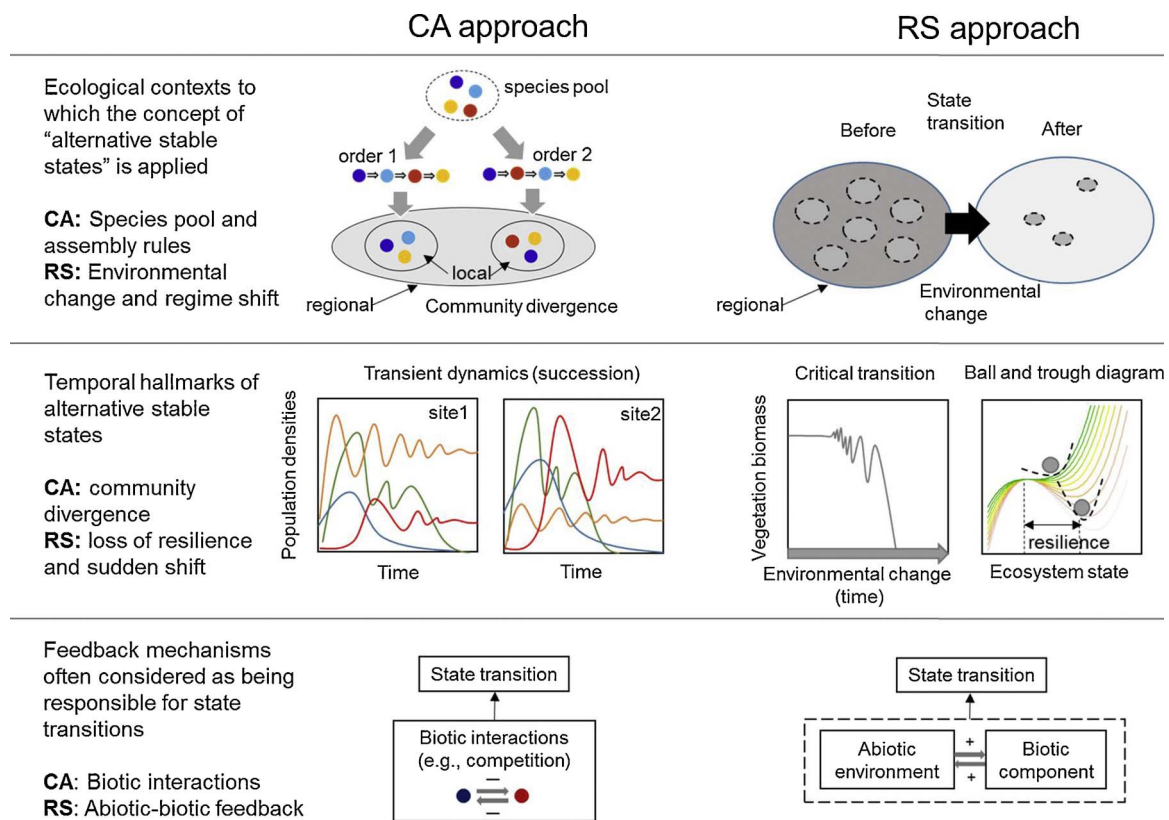


Fig. 1. Characteristics of the community assembly (CA) and regime shift (RS) approaches: (top row) ecological contexts to which the concept of “alternative stable states” is applied, (middle row) temporal hallmarks of alternative stable states; (bottom row) types of focal interactions that are shown to be responsible for the emergence of alternative state states. In the top-left panel, each dot represents a different species with different color, and the four species from regional species pool are assembled following two different immigration orders, leading to local community divergence. In the top-right panel, communities may exist in a patchy landscape and experience gradual environmental change, followed by the entire restructuring of the communities (e.g., loss of vegetation). In the middle-left panel, CA follows community divergence after long periods of transient dynamics, and results in different composition between the two sites. In the middle-right panel, vegetation biomass fluctuates to greater degrees as the catastrophic transition approaches (increased loss of resilience; ball and trough diagram), and collapses suddenly. In the bottom panels, the CA and RS approaches emphasize different sets of interactions as feedback mechanism that can drive state transitions. CA studies are often interested in competition among species (represented by blue and red balls) as positive biotic feedbacks, while RS studies often characterize state transition as a result of the feedback between abiotic environment and biotic components (such as community biomass).

2.3. Relevant interaction types

Feedback mechanisms are known to be key ingredients of alternative stable states and ecological restoration (Suding et al., 2004; Kéfi et al., 2016; but see Chapter 8 in Petraitis, 2013 for exceptions). The RS and CA studies consider different interaction types as feedback mechanisms that cause the emergence of alternative stable states (Fig. 1 bottom row). CA studies assume that, in the presence of strong interspecific competition, differences in species' abundances at the time when later colonists arrive determine which species outcompete the others (Kadowaki et al., 2012; Fig. 1). Such studies often ignore environmental changes and the feedbacks between abiotic and biotic factors (Fig. 1). In contrast, RS studies generally emphasize interactions between organisms and their abiotic environments (including ecosystem engineering) to represent positive feedbacks (Nishijima et al., 2016; Kéfi et al., 2016; Fig. 1). For instance, in shallow lakes, submerged macrophytes put down roots into lake-sediments, which suppresses the release of phosphorus into the water column. This rooting thereby maintains high water transparency and creates suitable conditions for their photosynthesis, which in turn enhances macrophyte growth. In contrast, phytoplankton suppresses the growth of submerged macrophytes, causing the release of phosphorus from bottom sediments into the water, further facilitating the growth of phytoplankton (Scheffer et al., 1993; Genkai-Kato and Carpenter, 2005). These self-reinforcing mechanisms cause alternative stable states in which either submerged plants or phytoplankton dominate in shallow lakes (Scheffer et al., 1993; Scheffer, 2004). In sum, CA and RS studies have focused on

different interaction types, suggesting together that both competition and facilitation may be important mechanisms for understanding alternative stable states.

2.4. Spatial scales studied

There is a general pattern that RS studies have often studied alternative stable states at much larger spatial scales than CA studies; whole ecosystems such as lakes (Persson et al., 2007; Carpenter et al., 2011) in the RS approach vs small-scale microcosms in the CA approach (Drake, 1991; Kadowaki et al., 2012). Interestingly, this contrasting pattern appears generally correlated with the focal interaction types as possible drivers of alternative stable states: facilitative interactions in RS studies, versus interspecific competition in CA studies. Theoretical studies resolve this gap by illustrating that alternative stable states at different spatial scales could occur because of the roles of different sets of biotic interactions. For instance, using a metacommunity model of two competitors, Shurin et al. (2004) showed that different interaction types can be responsible for alternative stable states at different spatial scales. In a two-species competition system, alternative stable states can occur at the local scale, because different species can win competition in different local sites via priority effects. Interspecific competition alone cannot create alternative stable states at the regional scale, however, because locally exclusive competitors can persist at the regional scale via competition-colonization trade-offs (i.e., the system has a single state corresponding to the coexistence of the two-species). When intraspecific facilitation is incorporated into the model as well such that

the two species facilitate their own persistence by modifying their environment, coexistence can be prevented both at the local and regional scales. As a result, including both facilitation and competition in the model can generate regional-scale alternative stable states (Shurin et al., 2004), with one species or the other dominating the whole region. Other theoretical studies also demonstrated that local facilitation is responsible for the generation of alternative stable states at large spatial scales (Takimoto, 2011; Xu et al., 2015). Thus, theoretical models emphasize that accounting for various interaction types at a range of spatial scales will improve our ability to capitalize on biotic interactions for ecological restoration.

3. Illustration using a toy model

In the previous section, we emphasized that the CA and RS approaches have focused on different resolutions of state variables, perturbation types, interactions types, and spatial scales. Here we use a simple ecological model to illustrate why and how the explicit consideration of some aspects of the CA approach can improve the use of RS approaches in ecological restoration. To this end, we develop a simple mathematical model that incorporates key aspects of both the CA approach (i.e., species identity and biotic interactions) into the RS approach. The model itself is not novel, but we use it to illustrate possible outcomes of integrating the two approaches for restoration. We chose a model that exhibits the two hallmarks of alternative stable states: divergence in community composition due to interspecific competition (i.e., CA approach), and the potential emergence of catastrophic regime shifts by incorporating positive abiotic feedback mechanisms (i.e., RS approach).

Our model consists of a two-species Lotka-Volterra competition model (Lotka 1925; Volterra 1928) with immigration, in which: (1) each species suffers from an additional mortality due to environmental deterioration, and (2) interspecific and intraspecific facilitation mitigate the effect of environmental change on elevated mortality (see Appendix S1 for more detailed description of the model). These two additions to the original Lotka-Volterra competition model correspond to characteristics of the RS approach: indeed, the model describes a situation where different species within a functional group compete for resources but can also facilitate each other in the face of environmental deterioration through habitat modification. For example, different submerged plant species in freshwater ecosystems compete for light and nutrients, but can simultaneously have a beneficial effect on each other through improved water transparency (Scheffer 2004). Also, woody plants in drylands do not only have competitive interactions with each other but also facilitative ones through improved stressful conditions (i.e., nurse plants) (Xu et al., 2015).

In the presence of strong interspecific competition, our model generates alternative stable states in the sense of the CA approach, which corresponds to states dominated by either species 1 or species 2 (see Fig. 2a and b respectively); indeed, the CA approach typically detects alternative stable states based on community divergence resulting from different initial conditions. Moreover, when interspecific and intraspecific facilitations are strong, the system exhibits a transition from a high to a low total abundance states with hysteresis in response to an increase in mortality (Fig. 2c); this fits the RS approach of alternative stable states focusing on the total abundance of both species as an aggregated measure of the system's state.

Our model reveals two significant insights regarding regime shifts and restoration. First, considering species identity and composition (i.e., distinguishing the two species within a community in our model) can improve our ability to forecast approaching regime shifts of community collapse. Fig. 2d shows that, in this model, total community abundance changes very slowly before the regime shift, but the relative species abundances exhibits a more pronounced, drastic change. Such a pattern occurs when the sensitivity to the environmental stress differs between species (the parameter setting used is shown in Appendix S1).

This result suggests that monitoring species composition or the population declines of specific species could help detecting that the system is approaching a threshold of community collapse.

Second, considering species identity can improve our ability to restore ecosystems because restoration success can depend upon the traits and order of the species being reintroduced. In our toy model, the reintroduction of the species with a lower tolerance to environmental stress or a lower intrinsic growth rate may fail to restore the community (Fig. 2e), whereas reintroducing species with a higher tolerance to environmental stress or a higher intrinsic growth rate under the same conditions can lead to successful recovery of the community (Fig. 2f). In other words, the identity of the species being reintroduced first can affect the outcome of restoration via effects mediated by species-specific ecological traits (e.g., tolerance to environmental deterioration, intrinsic population growth rate). The model clearly demonstrates the potential pitfalls in ecological restoration that could result from ignoring species identity and biotic interactions, both of which are key elements of the CA approach. Accounting for species identity and biotic interactions (a dominant driver of community assembly) allows us to identify indicator species that might signal the approaching state transition and enhance restoration feasibility of ecological community.

4. Integrative perspectives from empirical evidence

To go beyond the theoretical examination of the question, we now present two example case studies from the literature highlighting that incorporating key aspects of the CA approach (i.e., species identity and biotic interactions) into the RS approach will benefit ecological restoration in practice. The two case studies are chosen based on the criteria of being of specific relevance for ecological restoration, and illustrating potential key principles for merging the CA into RS approaches. We further propose that merging the CA approach (species traits and functional diversity) into the RS approach will bring novel insights that might improve the restoration of ecosystem functioning, by focusing on the relationship between alternative stable states and ecosystem functioning.

4.1. Integration of the CA and the RS approaches improves lake restoration

Lake eutrophication is well known to result from a catastrophic regime shift from a clear-water state with submerged plants to a turbid one with overabundant phytoplankton. In Japanese lakes, efforts to improve water quality, mainly by installing sewer systems, were made to restore the submerged macrophyte community which is key to restoring and maintaining the clear-water state. However, the improved water quality has sometimes run into new and unanticipated problems in light of the RS approach: the submerged macrophytes have been outcompeted by water chestnut (genus *Trapa*), an annual floating-leaved macrophyte (Fig. 3a). Although *Trapa* used to live in limited parts of the coastal areas before eutrophication (Nishihiro et al., 2014), its dominance after eutrophication drastically changed the dynamic state of communities and ecosystems of temperate lakes (Kato et al., 2016). The displacement of the submerged macrophytes by the floating-leaved plants probably occurs because the overabundance of phytoplankton generates organic sludge (i.e., accumulating dead phytoplankton) on bottom sediments over time, which constrains the germination and seedling establishment of submerged macrophytes. On the contrary, the large and solid seeds of *Trapa* spp. are capable of fixing on and becoming rooted in the fine-grained sludge at the bottom (Jun Nishihiro, personal communication; Fig. 3b, c). In some areas of the Lake Imbanuma, the removal of organic sludge on bottom sediments succeeded in reducing the floating-leaved plants and recovering the submerged plants (Fig. 3d, e), although it is a practical challenge to implement the removal of organic sludge at a whole lake scale.

This case study highlights that improved management of lake alternative stable states can depend not only on reestablishing the abiotic

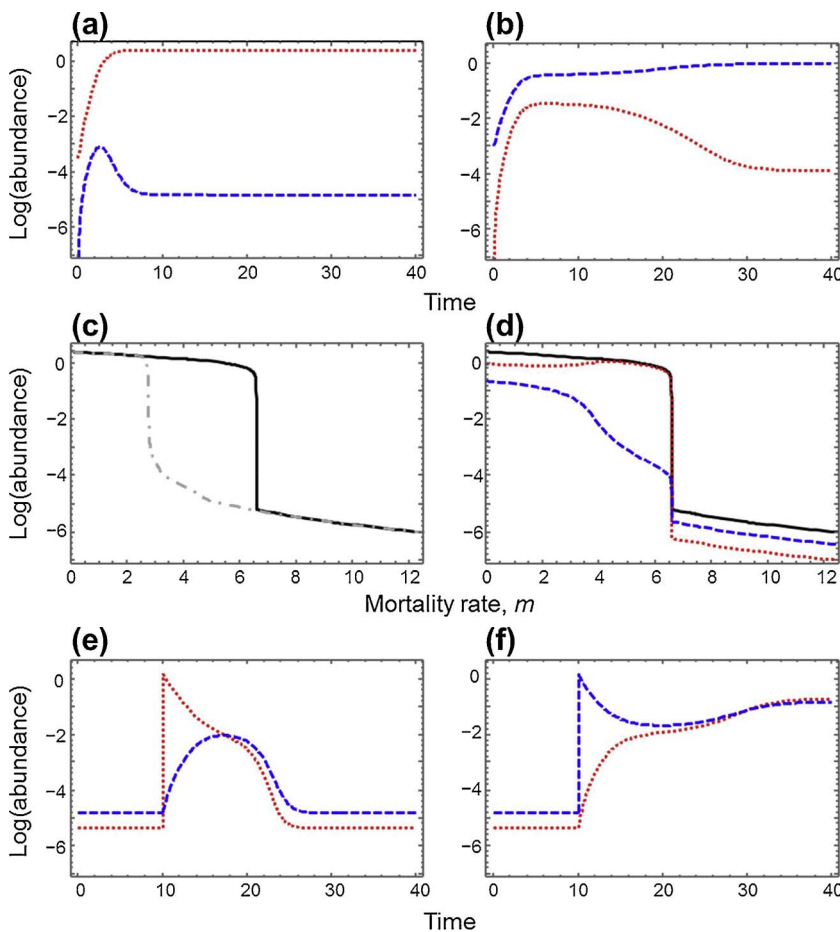


Fig. 2. Illustration of integration of the community assembly (CA) approach into the regime shift (RS) approach using a toy model. (a) (b) Alternative stable states generated by different initial conditions in the modified two-species Lotka-Volterra competition model. The red dotted and blue dashed lines indicate the abundances of species 1 and 2, respectively. (c) Changes in the total abundance (species 1 + species 2) when the mortality rate increases (black solid line) and decreases (gray dot-and-dash line) slowly. (d) Changes in total abundance (black, solid) and the abundances of species 1 (red, dotted) and species 2 (blue, dashed) when the mortality rate increases slowly. (e) (f) Context-dependencies of restoration failure (e) and success (f) defined by the order of species reintroduced (at $t = 10$). See Appendix S1 and Supplementary Mathematica code for details of the modeling.

feedbacks (i.e., improving water quality; the RS approach) but also on consideration and control of biotic feedbacks and community assembly mechanisms (i.e. competitive interactions between submerged and floating-leaved macrophytes; the CA approach). Importantly, the competitive superiority of the macrophytes changes depending on environmental conditions: submerged macrophytes dominate the floating-leaved plants before eutrophication, but this relationship reverses after eutrophication creates abundant organic sludge (dead phytoplankton) at the bottom. Therefore, the integration of RS and CA approach is crucial to successfully restore lakes covered by floating-leaved macrophytes.

4.2. Integration of the CA and the RS approaches improves terrestrial ecosystem restoration

Biomanipulation, which involves the removal or the (re)introduction of a species, can use the information on biotic interactions at play in the community of interest to facilitate recovery (Scheffer, 2004; Byers et al., 2006; Wolf et al., 2007; Roff and Mumby, 2012). Although the combination of biomanipulation and abiotic management has often been applied to shallow lakes (Scheffer 2004; Søndergaard et al., 2007), similar approaches may be useful for terrestrial restoration. In the floodplains of Yellowstone National Park, for example, facilitation between beavers and willows remained intact over long periods of time: willows provide food and dam materials for beavers, while beavers alter the physical environment and favor germination and establishment of willow species (Wolf et al., 2007). However, extinction of the top predators (wolves) profoundly affected the entire beaver–willow community through a long chain of abiotic and biotic interactions. Wolf extinction led to an increased red deer population, which increased grazing pressure on the willows. Without willows, a lack of food and

riverbank erosion led to a decline of beaver populations; as beaver dams were abandoned and accumulated sediments were severely eroded, the willow population decline accelerated. Although wolves were experimentally reintroduced in 1995, the willows did not initially recover because the decline of beaver populations reduced favorable sites (beaver dams) for willow establishment through severe riverbank erosion and such hydrological shift is irreversible (Wolf et al., 2007). This failure calls for a concerted effort to enforce wolf reintroduction (re-establishing biotic feedbacks; an action derived from the CA approach) and restore the hydrological regime (re-establishing abiotic feedbacks; an action derived from the RS approach) to restore the original beaver–willow state (Wolf et al., 2007). Species reintroduction via assisted colonization has generally been used to protect an endangered species, but it can sometimes also serve as an integrated management tool to restore a whole ecological community, although unwanted risks of re-introduction should always be managed.

4.3. Alternative stable states and ecosystem functioning

The integration of CA and RS approaches may have important implications for restoring ecosystem functioning. In recent years, several empirical studies have begun to demonstrate that environmental change affects community assembly, which could also influence ecosystem functioning via alterations in species composition (Maherali and Klironomos, 2007; Dickie et al., 2012; Kardol et al., 2013). When accounting for potential effects of environmental change on ecosystem functioning, alternative stable states in community composition might be critical since a sudden and irreversible state transition from one community state to another will lead to a transition of ecosystem functioning as well. While previous studies have pointed to the consequences of alternative stable states for ecosystem functioning

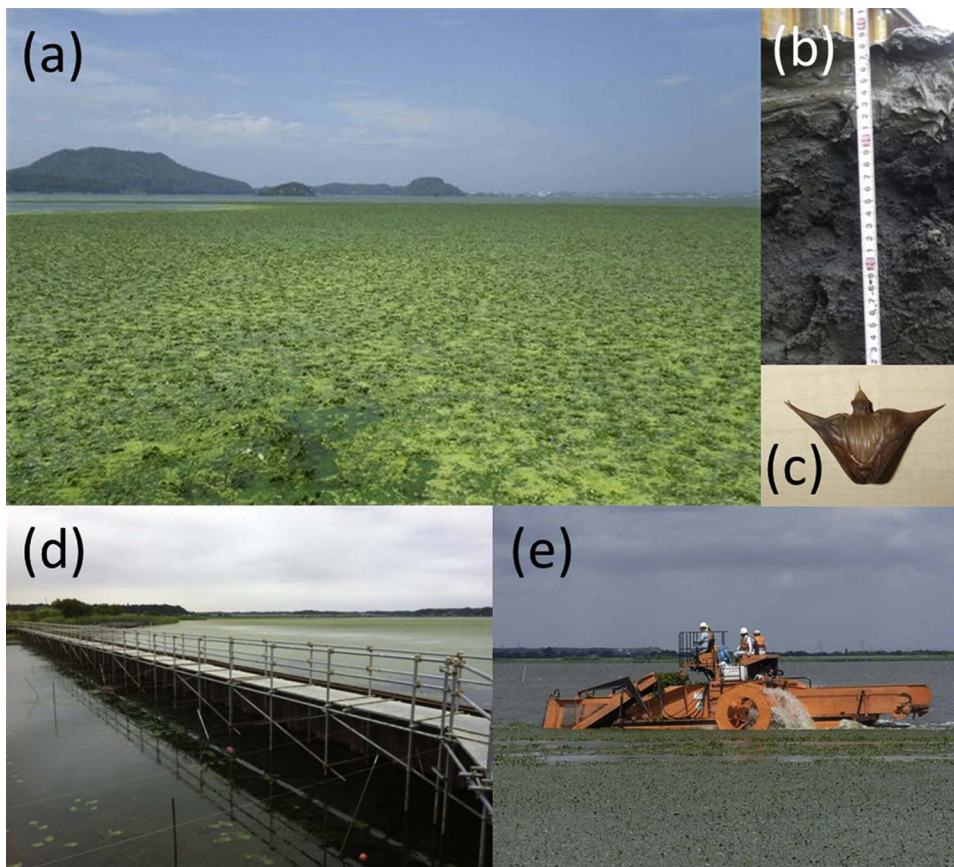


Fig. 3. (a) Lake Koyama-ike with overabundant *Trapa japonica*. (b) Accumulated organic sludge on top of the bottom sediment of Lake Imbanuma. (c) Seed of *T. japonica*. (d, e) Restoration experiment in Lake Imbanuma by (d) removing organic sludge on the near side of the barrier and (e) removal of *Trapa natans* var. *japonica*. Photo credits: (a, b, c, e) Jun Nishihiro, (d) S. Nishijima.

(Eldridge et al., 2011; Oliver et al., 2015), our new perspective—integrating the CA approach into the RS approach—will help explicitly link state transitions of community states to those of ecosystem functioning.

Here we illustrate key predictions of alternative “ecosystem functioning” states following environmental change based on merging CA theory into the RS approach, using one example graphical diagram (Fig. 4). Let us start from a diagram of alternative stable states, where community state is plotted as a function of environmental harshness (Fig. 4a). To derive predictions of ecosystem functioning using our framework, we focus on three scenarios about the link between community states and ecosystem functioning. As a special case, when ecosystem functioning is independent of changes in community state, there

should be no alternative stable states in ecosystem functioning (black horizontal lines in Fig. 4b, c). In contrast, alternative “ecosystem functioning” states may occur if alternative community states are composed of species that are functionally different; and in this case, the two scenarios are likely. Depending on whether the relationship between community states and ecosystem functioning can be described by a convex-down (green curves in Fig. 4b) or concave-up (orange curves in Fig. 4b) curve, the form of the hysteretic responses of ecosystem functioning after increased environmental harshness will also vary (Fig. 4c). It will be more difficult to predict state transitions of ecosystem functioning with a concave-up curve, since there would then be small changes in ecosystem functioning before the state transition.

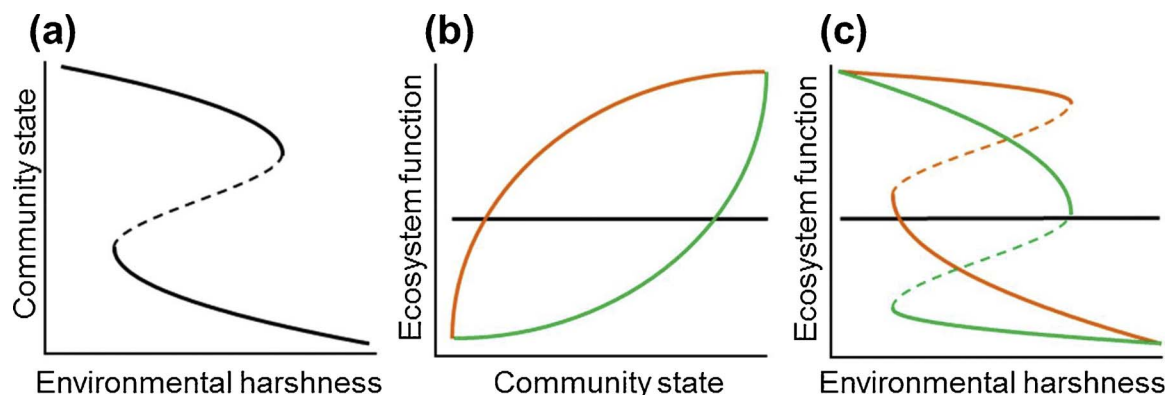


Fig. 4. Alternative stable states of ecosystem functioning in view of the integration of the CA approach into the RS approach. (a) If we assume that a community state (e.g., species richness) has alternative stable states at intermediate levels of a given environmental harshness, increasing harshness triggers a regime shift to the degraded community state. As a special case, when ecosystem function is independent of community states (horizontal line in b) due to complete functional redundancy, environmental deterioration does not cause a regime shift at the level of ecosystem function (black horizontal line in c). Depending on whether ecosystem function is described as a concave-up (orange) or convex-down (green) function (orange and green solid curves in b), the consequences of increased environmental harshness differ greatly between the two functional forms (orange and green solid-and-dotted curves respectively in c).

Thus, the graphical diagram suggests that the form of community state-ecosystem functioning relationship can be used to predict when ecosystem functioning transitions to a new state after environmental change. Since species functional traits and environmental conditions play a role in shaping ecosystem functioning (Zirbel et al., 2017), we suggest that the integrated CA-RS approach could provide a novel understanding of alternative stable states (Tomimatsu et al., 2013), and will improve our knowledge and prediction about how state transitions affect ecosystem functioning in changing environments. We do not know of any restoration studies that have gone into this direction, but some evidence shows that alternative “community” states do not necessarily correspond to alternative “ecosystem functioning” states if the community shows functional redundancy and compensation. For instance, in a wood-decaying fungal community, differences in species composition caused by different immigration histories do not create significant differences in decomposition rates because of functional redundancy (Dickie et al., 2012).

5. Conclusions

Ecosystems that exhibit alternative stable states are a prominent challenge for ecosystem restoration. Here, using a review of the literature and a simple model, we highlight how, and under what conditions, understanding processes typically addressed only in the CA approach can improve ecological restoration guided by the RS approach. Particularly, accounting for the CA approach can allow us to identify indicator species that might exhibit characteristic dynamics prior to the state transition and enhance the restoration of ecological communities more effectively than by simply relying on the RS approach. We suggest that future efforts to restore feedback mechanisms involving both abiotic environmental conditions and biotic interactions should consider important aspects of community assembly. Such integrated perspective will be crucial for broadening our ability to manage alternative stable states and improving the prediction of regime shifts, particularly in the face of global environmental change.

Acknowledgments

We thank Phil Stephens, Peter Petraitis, Gerlinde de Deyn, Shiqiang Wan and two anonymous reviewers for insightful comments on the manuscript. We are grateful for a Japan Society for the Promotion of Science (JSPS) Research Fellowship (no. 13J02732) and Grants-in-Aid for Scientific Research B (no. 15H05249) (KK), funding from the Environment Research and Technology Development Fund (S-14) of the Ministry of the Environment and a Grant-in-Aid for Young Scientists Start-up (no. 17H07413) (SN), the Centre National de la Recherche Scientifique, and the European Union's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 283068 (CASCADE) (SK), Center for Ecological Research, Kyoto University as an affiliated scientist, a Grant-in-Aid for Young Scientists B (no. 16770025) and the River Fund in charge of the Foundation of River and Watershed Environment Management (FOREM), the Collaborative Research of Lake Biwa Museum (KOK), and a Grant-in-Aid for Young Scientists A (no. 25712036) from the Ministry of Education, Culture, Sports, Science and Technology of Japan (TS).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolind.2017.11.035>.

References

Baer, S.G., Blair, J.M., Collins, S.L., 2015. Environmental heterogeneity has a weak effect on diversity during community assembly in tallgrass prairie. *Ecol. Monogr.* 86, 94–106.

- Beisner, B.B., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* 1, 376–382.
- Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks, J.A., Wilson, W.G., 2006. Using ecosystem engineers to restore ecological systems. *Trends Ecol. Evol.* 21, 493–500.
- Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Litchell, J.F., Seekell, D.A., Smith, L., Weidel, B., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332, 1079–1082.
- Chang, C., HilleRisLambers, J., 2016. Integrating Succession and Community Assembly Perspectives. <http://dx.doi.org/10.12688/f1000research.8973.1>. (5:F1000 Faculty Rev-2294).
- Chase, J.M., 2003. Community assembly: when should history matter? *Oecologia* 136, 489–498.
- Dickie, I.A., Fukami, T., Wilkie, J.P., Allen, R.B., Buchanan, P.K., 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecol. Lett.* 15, 133–141.
- Didham, R.K., Norton, D.A., 2007. Alternative logical states. *Oikos* 116, 358–360.
- Drake, J.A., 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *Am. Nat.* 137, 1–26.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14, 709–722.
- Fukami, T., Bezemer, T.M., Mortimer, S.R., van der Putten, W.H., 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecol. Lett.* 8, 1283–1290.
- Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Ann. Rev. Ecol. Syst.* 46, 1–23.
- Genkai-Kato, M., Carpenter, S.R., 2005. Eutrophication due to phosphorus recycling in relation to lake morphometry, temperature, and macrophytes. *Ecology* 86, 210–219.
- Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D., Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518, 94–97.
- Hobbs, R.J., Cramer, V.A., 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annu. Rev. Environ. Resour.* 33, 39–61.
- Hobbs, R.J., 2007. Setting effective and realistic restoration goals: key directions for research. *Restor. Ecol.* 15, 354–357.
- Isbell, F., Tilman, D., Polasky, S., Binder, S., Hawthorne, P., 2013. Low biodiversity state persists two decades after cessation of nutrient enrichment. *Ecol. Lett.* 16, 454–460.
- Kéfi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A., de Ruiter, P.C., 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449, 213–217.
- Kéfi, S., Holmgren, M., Scheffer, M., 2016. When can positive interactions cause alternative stable states in ecosystems? *Funct. Ecol.* 30, 88–97.
- Kadowaki, K., Inouye, B.D., Miller, T.E., 2012. Assembly-history dynamics of a pitcher-plant protozoan community in experimental microcosms. *PLoS One* 7, e42651.
- Kardol, P., Souza, L., Classen, A.T., 2013. Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos* 122, 84–94.
- Kato, Y., Nishihiro, Y., Yoshida, T., 2016. Floating-leaved macrophyte (*Trapa japonica*) drastically changes seasonal dynamics of a temperate lake ecosystems. *Ecol. Res.* 31, 695–707.
- Ling, S.D., Johnson, C.R., Frusher, S.D., Ridgway, K.R., 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proc. Natl. Acad. Sci. U. S. A.* 106, 22341–22345.
- Lotka, A.J., 1925. *Elements of Physical Biology*. Williams and Wilkins, Baltimore.
- Maherali, H., Klironomos, J.N., 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316, 1746–1748.
- Martin, K.L., Kirkman, K.L., 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. *J. Appl. Ecol.* 46, 906–914.
- Nishihiro, J., Kato, Y., Yoshida, T., 2014. Heterogeneous distribution of a floating-leaved plant, *Trapa japonica*, in Lake Mikata, Japan, is determined by limitations on seed dispersal and harmful salinity levels. *Ecol. Res.* 29, 981–989.
- Nishijima, S., Takimoto, G., Miyashita, T., 2016. Autochthonous or allochthonous resources determine the characteristic population dynamics of ecosystem engineers and their impacts. *Theor. Ecol.* 9, 117–127.
- Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., et al., 2015. Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* 30, 673–684.
- Persson, L., Amundsen, P.A., de Roos, A.M., Klemetsen, A., Knudsen, R., Primicerio, R., 2007. Culling prey promotes predator recovery—alternative states in a whole-lake experiment. *Science* 316, 1743–1746.
- Petraitis, P., 2013. *Multiple Stable States in Natural Systems*. University Press, Oxford.
- Robinson, J.F., Dickerson, J.E., 1987. Does invasion sequence affect community structure? *Ecology* 68, 587–595.
- Roff, G., Mumby, P.J., 2012. Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.* 27, 404–413.
- Søndergaard, M., Jeppesen, E., Lauridsen, T.L., Skov, C., van Nes, E.H., Roijackers, R., Lammens, E., Portielje, R., 2007. Lake restoration: success, failures and long-term effects. *J. Appl. Ecol.* 44, 1095–1105.
- Sasaki, T., Okayasu, T., Jamsran, U., Takeuchi, K., 2008. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. *J. Ecol.* 96, 145–154.
- Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M., Mori, A.S., 2015. Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecol. Indic.* 57, 395–408.

- Scheffer, M., Carpenter, S., 2003. Catastrophic regime shifts in ecosystems linking theory to observation. *Trends Ecol. Evol.* 18, 648–656.
- Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8, 275–279.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Scheffer, M., 2004. *Ecology of Shallow Lakes*. Kluwer Academic Press.
- Shurin, J.B., Amarasekare, P., Chase, J.M., Holt, R.D., Hoopes, M.F., Leibold, M.A., 2004. Alternative stable states and regional community structure. *J. Theor. Biol.* 227, 359–368.
- Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.* 24, 271–279.
- Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53.
- Takimoto, G., 2011. Local-regional richness relationships and alternative stable states in metacommunities with local facilitation. *Theor. Ecol.* 4, 385–395.
- Tomimatsu, H., Sasaki, T., Kurokawa, H., Bridle, J.R., Fontaine, C., Kitano, J., Stouffer, D.B., Vellend, M., Bezemer, T.M., Fukami, T., et al., 2013. Sustaining ecosystem functions in a changing world: a call for an integrated approach. *J. Appl. Ecol.* 50, 1124–1130.
- van de Koppel, J., Rietkerk, J.M., Weissing, F.J., 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol. Evol.* 12, 352–356.
- Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. *ICES J. Mar. Sci.* 3, 3–51.
- Walker, B.H., Carpenter, S.R., Rockstrom, J., Crepin, A.S., Peterson, G.D., 2012. Drivers, slow variables, fast variables, shocks and resilience. *Ecol. Soc.* 17, 30.
- Wolf, E.C., Cooper, D.J., Hobbs, N.T., 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecol. Appl.* 17, 1572–1587.
- Xu, C., Van Nes, E.H., Holmgren, M., Kéfi, S., Scheffer, M., 2015. Local facilitation may cause tipping points on a landscape level preceded by early-warning indicators. *Am. Nat.* 186, E81–E90.
- Young, T.P., Chase, J.M., Huddleston, R.T., 2001. Community succession and assembly comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecol. Restor.* 19, 5–18.
- Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol. Lett.* 8, 662–673.
- Zirbel, C.R., Bassett, T., Grman, E., Brudvig, L.A., 2017. Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *J. Appl. Ecol.* 54, 1070–1079.